Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: Implications for offshore predators

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We estimated the biomass of deepwater demersal forage fishes (those species common in the diets of lake trout and Chinook salmon) in Lake Huron during the period 1994–2007. The estimated total lake-wide biomass of deepwater demersal fishes in 2007 was reduced by 87 percent of that observed in 1994. Alewife biomass remained near the record low observed in 2004. Biomass of young-of-the-year rainbow smelt was at a record high in 2005, but little recruitment appears to have occurred in 2006 or 2007. Record-high estimates of young-of-the-year bloater biomass were observed in 2005 and 2007, and an increase in the biomass of adult bloater in 2007 suggests that some recruitment may be occurring. The biomass of other potential deepwater demersal forage fish species (sculpins, ninespine stickleback, trout-perch and round goby) has also declined since 1994 and remained low in 2007. The forage fish community in 2007 was dominated by small (<120 mm) bloater and rainbow smelt. These results suggest that lake trout and Chinook salmon in Lake Huron may face nutritional stress in the immediate future.

Keywords: fish community, alewife, rainbow smelt, bloater, Great Lakes foodwebs

Introduction

The native deepwater demersal fish community in Lake Huron supported lake trout *Salvelinus namaycush* and burbot *Lota lota* as main predators, which primarily fed on a number of species of deepwater ciscos *Coregonus* spp. and sculpins *Cottus* spp. and *Myoxocephalus thompsoni* (Eshenroder and Burnham-Curtis, 1999). Other species that occurred in the deep waters of the lake include lake whitefish *Coregonus clupeaformis*, round whitefish *Prosopium cylindraceum*, ninespine stickleback *Pungitius pungitius*, trout-perch *Percopsis omiscomaycus*, spottail shiner *Notropis hudsonius*, lake chub *Coeusius plumbeus*, white sucker *Catostomus commersoni*, and longnose sucker *Catostomus catostomus* (Argyle 1982; Spangler and Collins, 1992; Ebener et al., 1995).

The Lake Huron deepwater demersal fish community has undergone many changes over the past century (Ebener et al., 1995; Riley et al., 2008), among the most significant of which were the invasion of rainbow smelt (*Osmerus mordax*) in the 1920s, followed by alewife (*Alosa pseudoharengus*) and sea lamprey (*Petromyzon marinus*) in the 1930s. Sea lamprey predation and overfishing led to the collapse of lake trout by the 1950's in most of Lake Huron, and many of the original deepwater cisco species in Lake Huron were extirpated by 1960 (Smith and Todd, 1984; Roseman et al., this volume). Sea lamprey control that began in the 1960s continues to the present and has allowed the survival of stocked Pacific salmon *Oncorhynchus* spp. and lake trout, which have supported popular and valuable recreational fisheries since the 1970s.

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In the 1990s the invasion of zebra and quagga mussels (*Dreissena* spp.) changed the Lake Huron ecosystem significantly. Although the mechanisms are not well understood, these new invasive species appear to have altered foodwebs, with potentially far-reaching consequences to the deepwater fish community (Hecky et al., 2004; McNickle et al., 2006). The most recent introduced fish species is the round goby (*Apollonia melanostoma*), which is benthic and may compete with native fishes such as sculpins (Jude and DeBoe, 1996).

The physical and biological components of the Lake Huron ecosystem have undergone rapid and unprecedented change over the past several years. In Saginaw Bay, water clarity has increased, chlorophyll has declined, macrophytes have increased, and the benthic macroinvertebrate community has shifted (Fahnenstiel et al., 1995; Budd et al., 2001, Nalepa et al., 2003). In the main basin of the lake, abundance of the benthic amphipod *Diporeia* sp. has declined dramatically (Nalepa et al., 2005, 2007), zooplankton abundance has declined and community dominance has shifted from cladocerans to calanoid copepods (M. Balcer, University of Wisconsin-Superior, Superior, WI, pers. comm.; R. Barbiero, USEPA GLNPO, Chicago, IL, pers. comm.), deepwater demersal fish abundance and biomass have drastically declined (Riley et al., in press), natural reproduction of lake trout has been widely observed for the first time in decades (Riley et al., 2007), abundance, size-at-age, and condition of lake whitefish have decreased (Mohr and Ebener, 2005), and Chinook salmon condition and harvest have declined (J.E. Johnson, Michigan Department of Natural Resources, Alpena Fisheries Station, Alpena, MI, pers. comm.). Here we describe changes in biomass of the dominant demersal forage fish species in the Michigan waters of Lake Huron from 1994–2007.

Methods

The USGS Great Lakes Science Center (GLSC) has conducted annual bottom trawl surveys on Lake Huron since 1973 (Riley et al., 2008). Here we focus on data collected during 1994–2007 using a 21-m wing trawl with 4.76 mm square cod end mesh. Sampling was conducted annually during this time period, except during 2000 when sampling did not occur due to vessel breakdown. Data from 1998 were suspect and were not included here.

Trawl sampling was performed annually in late October through early November at five ports in U.S. waters: Detour, Hammond Bay, Alpena, Au Sable Point (Tawas), and Harbor Beach (Figure 1). At each port, 10-minute on-contour trawl tows are made at fixed transects from 9 to 110 m in depth. The number of transects varies among ports due to variation in bathymetry and bottom composition. Sampling also occurred at Goderich, Ontario during 1999 and 2003-2007 (Figure 1).

We applied correction factors to standardize trawl data among depths, as the actual time on bottom for each trawl increased with depth (Fabrizio et al., 1997). For each species, biomass per 10 min on bottom was estimated as:

$$B = \frac{10W}{KT},$$

where B is the biomass per 10 min on bottom, 10 is a scaling factor, W is the weight of fish captured, T is tow time, and K is a correction factor that varies with fishing depth (D in m) such that $K = 0.00385\mathrm{D} + 0.9149$. Catches were expressed in terms of biomass (kg ha^{-1}) by dividing B by the area swept by the trawl. The area swept was estimated as the product of the distance towed (speed multiplied by tow time) and the trawl width. Total lakewide biomass for depths between 9 and 100 m was estimated as:

$$LB_i = \sum_{s=0}^{s=110} \frac{W_{is} a_s}{n}$$

where LB_i is lakewide biomass of species i, W_{is} represents mean biomass (kg ha^{-1}) of each species within each depth stratum s, a_s represents the weighted area (Ha^2) of individual strata s estimated from the Lake Huron GIS, and n represents the number of depth strata.

Riley et al. (2008) defined common species of the Lake Huron deepwater demersal fish community as those that were captured in at least ten percent of all trawls. Here we focus on a subset of these species: forage fish (rainbow smelt, alewife, bloater, deepwater sculpin, trout-perch, ninespine stickleback, slimy sculpin *Cottus cognatus*, and round goby), which we define as those species that typically comprise over 90% of trawl biomass and are likely to serve as important prey for lake trout and Chinook salmon, the primary offshore predators in the lake.

For alewife, rainbow smelt, and bloater, biomass was apportioned into age-0 and adult fish based on length frequency data from all tows where a species

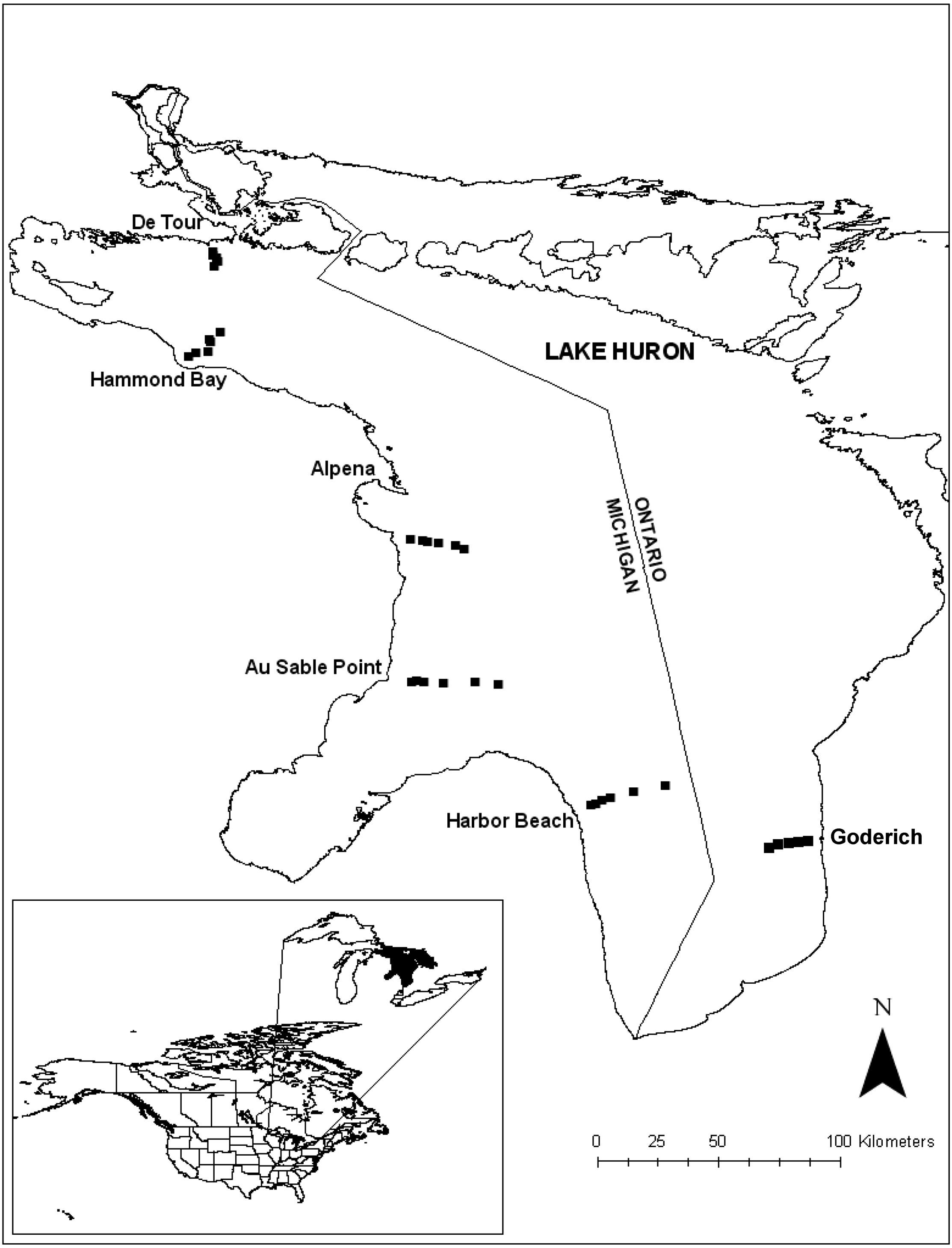

Figure 1. Bottom trawl sampling locations in Lake Huron. All U.S. ports were sampled using a 21-m wing trawls from 1992–2007 while Goderich, ON was sampled during 1998, 1999, and 2003–2007. Trawl depths ranged from 9 to 110 m.

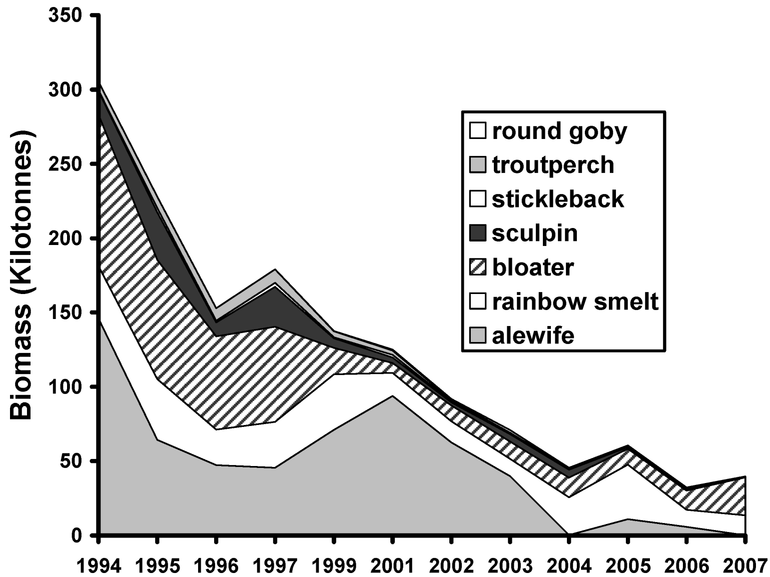

Figure 2. Mean total biomass (kt) of deepwater demersal fish species in the main basin waters of Lake Huron, 1994–2007. Abscissa scale is not continuous.

was captured. We used 100 mm total length as a demarcation between juvenile and older fish for alewife, 90 mm for rainbow smelt, and 120 mm for bloater based on historical age-length relationships (USGS unpublished data).

Results

The estimated total lakewide biomass of deepwater demersal forage fishes in Lake Huron has declined since 1994, primarily due to reductions in alewife and bloater biomass (Figure 2). The estimated total lakewide biomass of deepwater demersal forage fishes in 2007 was 87 percent lower than that observed in 1994.

Adult alewife biomass was fairly stable from about 1995 through 2002, decreased dramatically in 2003 and has remained low since (Figure 3a). Age-0 alewife biomass was low during the 1990s, peaked in 2001 and again in 2003, and has remained fairly low since (Figure 3a). The large numbers of young-of-the-year alewife observed in 2001 and 2003 do not appear to have recruited to the adult population. Between 2003 and 2007, alewife size distribution has been dominated by fish less than 100 mm TL as shown for 2007 (i.e. age-0 fish; Figure 4). Recent year-classes either failed to survive (2003) or were present at low densities (2004–2007).

Adult rainbow smelt biomass was highest in 1994 and has declined over the time series (Figure 3b). Age-0 rainbow smelt biomass has fluctuated over the time series but showed a record high in 2005 (Figure 3b). The rainbow smelt population has been dominated by age-0 fish in recent years typically with less than 10% of the population larger than 100 mm (Figure 4). The low biomass of adult fish in 2007 suggests that the large numbers of small rainbow smelt observed in 2005 and 2006 did not translate into recruitment of larger rainbow smelt. In fact, the combined biomass for all age classes of rainbow smelt decreased by about 50% from 2005 to 2006-2007 despite the record-high biomass of age-0 fish observed in 2005.

Relatively high biomass estimates for young-of-the-year bloater were observed in 2005 and 2007; the biomass estimated for 2007 was an order of magnitude greater than any estimate prior to 2005 (Figure 3c). Adult bloater biomass was highest in 1994 and has declined markedly since then, although adult biomass has increased since 2005 (Figure 3c), suggesting that some recruitment has occurred from the high biomass of small bloater observed in 2005.

The biomass of slimy (Figure 3d) and deepwater (Figure 3d) sculpins in Lake Huron have decreased dramatically since 1994; deepwater sculpin biomass in 2007 was less than one percent of the estimate in 1994, and no slimy sculpins were captured in 2007. Biomass of round gobies increased after their initial capture until 2003, when it began to decline to current low levels (Figure 3d). Biomass of ninespine

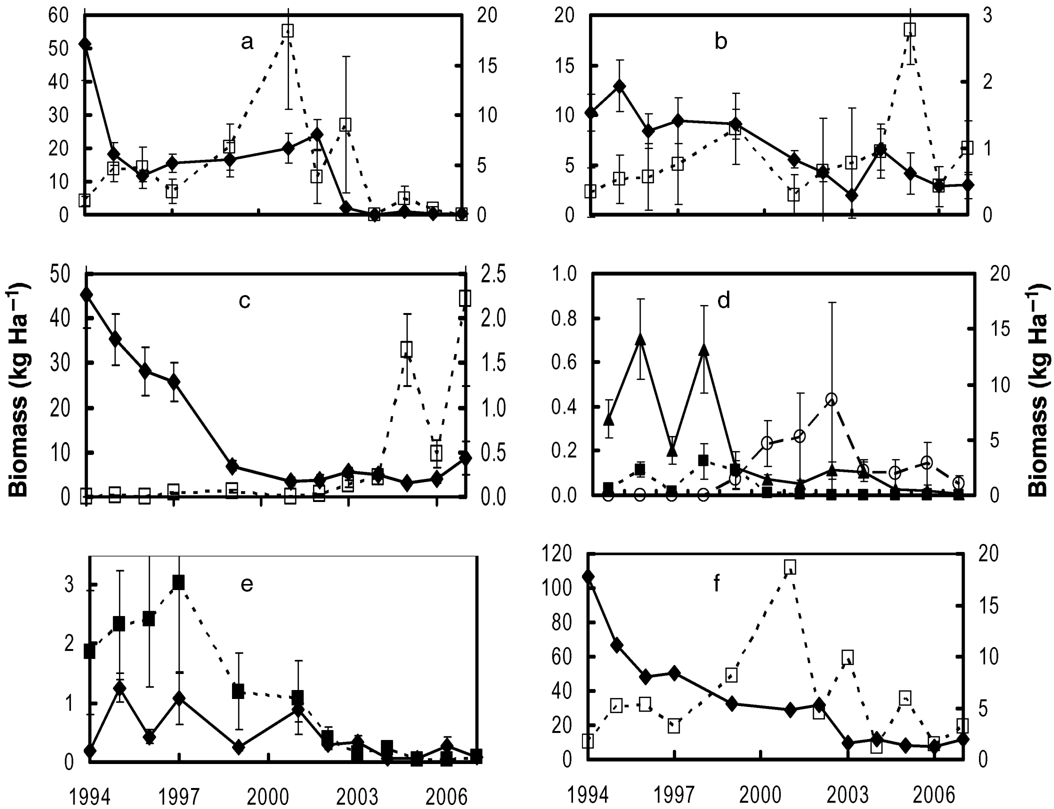

Figure 3. Mean biomass (kg ha^{-1}) of a) young-of the-year (solid line) and adult (dashed line) alewives b), young-of the-year (solid line) and adult (dashed line) rainbow smelt, c) young-of the-year (solid line) and adult (dashed line) bloater, d)slimy sculpin (solid line solid squares), round goby (dashed line open circles), and deepwater sculpin (solid line triangles) e) troutperch (dashed line) and nine-spine stickleback (solid line) (f) young-of the-year (solid line) and adult (dashed line) totals for alewife, rainbow smelt, and bloater combined in the main basin waters of Lake Huron, 1994–2007. Note that young-of the-year data are expressed on the right axis in panels a, b, c, and f while deepwater sculpin are expressed on the right axis in panel d. Error bars are two standard errors of the mean.

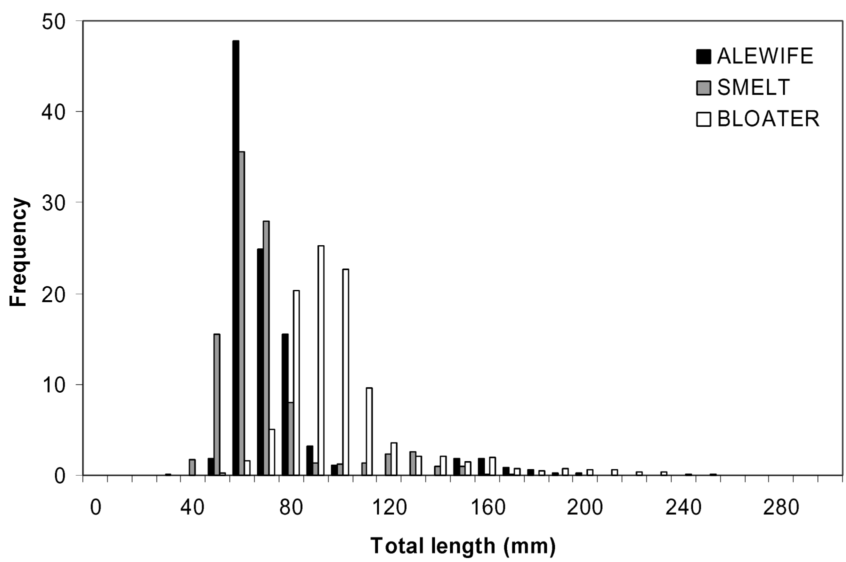

Figure 4. Length-frequency histograms for alewife, rainbow smelt and bloater captured by the USGS fall bottom trawl survey in Lake Huron, 2007.

sticklebacks have has declined since 1994 (Figure 3e). Trout-perch biomass has continued to decline since 1994, and biomass remains low for the time series (Figure 3e).

The combined biomass of yearling-and-older alewife, smelt, and bloater, traditionally the three most abundant species in the lake, has been decreasing steadily since 1994; combined biomass increased somewhat since 2006 but remains at only slightly more than 10 percent of the value observed in 1994 (Figure 3f). By contrast, the total biomass of young-of-the-year of these three species was low in 1994, reached a peak of over ten times the 1994 estimate in 2001, and has declined since then to levels similar to those observed in 1994–1997 (Figure 3f). No other species have replaced this lost biomass.

Discussion

Riley et al. (2008) suggested that the deepwater demersal fish community in Lake Huron was undergoing collapse through 2006. With the exception of bloater, data from 2007 confirm that biomass of adults of most species remain very low. Biomass of juvenile rainbow smelt was at an all-time high in 2005, but little recruitment of these small fish appears to have occurred. Record-high estimates of young-of-the-year bloater biomass were observed in 2005 and 2007, and an increase in the biomass of adult bloater in 2007 suggests that some recruitment may be occurring. Several factors might be responsible for the observed changes in the Lake Huron deepwater demersal fish community, including the effects of multiple exotic species, increased predation by fish or cormorants, fisheries, physical factors (e.g. climate change, nutrients), or disease. Unfortunately, long-term data on the majority of these factors are lacking for Lake Huron. Thus, despite extensive long-term sampling, we were not able to quantitatively determine the factors that contributed to the observed community changes, which highlights the need for comprehensive monitoring across all trophic levels. Speculation regarding the causes of the dramatic changes in biomass of deepwater demersal fish species in Lake Huron is currently difficult because of a lack of published data on several important components of the ecosystem (Riley et al., 2008).

While a reduction in the biomass of exotic species, such as alewife and rainbow smelt, is consistent with fish community objectives for Lake Huron (DesJardine et al., 1995), the availability of prey and the sustainability of sport fisheries for lake trout and Chinook salmon are concerns for fisheries managers and stakeholders (Dobiesz et al., 2005). The total biomass of adult alewife, rainbow smelt, and bloater, which are the most common prey of lake trout (Madenjian et al., 1998) and Chinook salmon (Diana,1990), remains low, although a slight increase in combined biomass was evident in 2007. The combined biomass of young-of-the-year adult alewife, rainbow smelt, and bloater began to increase after 1997 and has been characterized by semiannual peaks of decreasing amplitude since 2001, but these large peaks in biomass appear to have resulted in little recruitment, with the possible exception of bloater. The biomass of other potential prey species (sculpins, ninespine stickleback, trout-perch and round goby) also remained low in 2007. The continued low biomass of these forage fish species is likely to have serious implications for the growth and survival of offshore predators such as lake trout and Chinook salmon. The fact that angler catch rates for Chinook salmon have declined in recent years (J.E. Johnson, Michigan Department of Natural Resources, Alpena Fisheries Station, Alpena, MI, pers. comm.) is not surprising given these results.

Young-of-the-year alewife, rainbow smelt and bloater are more pelagic than older age-classes of these species (Argyle, 1982), and the very large but sporadic increases in biomass observed for these species may indicate that current physical (e.g. increased water clarity) and biological conditions (e.g. low alewife abundance) may be promoting the survival of pelagic or nearshore fish species over offshore demersal species in Lake Huron. Schaeffer et al. (2008) observed very high densities of emerald shiner (a pelagic species) using hydroacoustics in Lake Huron in 2006, and repeated record year-classes of walleye and yellow perch have been observed in recent years in Saginaw Bay (Fielder et al., 2007).

Our fish biomass estimates are likely to be biased because bottom trawling does not sample the entire water column and pelagic individuals of any species are unlikely to be captured (Argyle, 1982; Stockwell et al., 2006). This is particularly true for young-of-the-year alewife, rainbow smelt and bloater (which are pelagic at some times); biomass estimates for these species are particularly suspect, as reflected in the large error associated with the recent high abundances observed (Figure 3). The fact that some transects and ports (Goderich) were not sampled in some years will also affect the reliability of year-to-year comparisons of fish biomass. Estimates of biomass reported here are likely to be biased and should be interpreted with caution. However, the large magnitude of change in forage fish community biomass (87%) observed over the 13 year time period indicates that major changes have occurred.

The potential responses of top predators to changes in Great Lakes ecosystems are complex and difficult to predict (Kitchell et al., 2000). The recent depression of deepwater demersal forage fish biomass in the main basin of Lake Huron suggests that lake trout and Chinook salmon may face nutritional stress in the immediate future. As discussed above, evidence of this is already apparent in reduced growth and catch rates of Chinook salmon. Continued monitoring of the deepwater demersal fish community in Lake Huron is recommended.

Conclusions

Herein we report evidence of drastic declines in the abundance of a majority of deepwater demersal fish species in one of the world's largest lakes; but these declines are not limited to a single trophic level. The extent and scope of these changes suggest that the deepwater demersal fish community may be collapsing. The question of which factors are responsible for these recent changes is currently difficult to answer because no long-term published data are available on several key factors (e.g. annual abundance of Chinook salmon, phytoplankton, zooplankton, Dreissenid mussels and other benthic invertebrates) that might be important. The timing of the changes suggests that the recent invasion of the lake by multiple exotic species at several trophic levels may be a major causative factor responsible for these recent declines, but confirmation of this hypothesis is hindered by a lack of long-term data on trends in abundance of other species in Lake Huron. Long-term monitoring of multiple trophic levels in the lake is needed to understand the causes and magnitude of the recent changes in the deepwater fish community. The effects of continued change in this community on future ecosystem function, including fisheries for lake whitefish, lake trout, and Pacific salmon, are difficult to predict.

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